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Patterns of activity cycles in juvenile California two-spot octopuses (*Octopus bimaculoides*)

David L. Sinn

School of Zoology, University of Tasmania, Private Bag 5, Hobart, Tasmania 7001, Australia, david.sinn@utas.edu.au

Abstract: Octopuses function as important prey and predators in many continental-shelf marine ecosystems. Understanding activity cycles of octopuses should help define their mode of foraging and potential resource utilization and, therefore, their niche within the marine community. Unfortunately, little is known concerning activity cycles of octopuses, especially during their juvenile life-history stages. Here, I present observations on juvenile activity in *Octopus bimaculoides* Pickford and McConnaughey, 1949 over three observational weeks in a semi-natural laboratory setting. Octopuses on average were nocturnal, but some individuals were active during daylight hours in all three observational weeks. Nocturnal activity cycles may decrease the risk of predation on juveniles by visual fish predators hunting during daylight hours. However, inter- and intraspecific competition with other octopuses in different life history stages, including adult *O. bimaculoides* and adult and juvenile *Octopus bimaculatus* Verrill, 1883 is also likely during nighttime hours. Further studies are needed on the relative influence of predation and competition on octopus activity cycles and the resulting consequences for octopus populations.

Key words: cephalopod, octopus activity, juvenile ecology, niche partitioning

Activity cycles play an important role in determining a species' niche. At the individual level, an organism's activity cycle mediates the ecological trade-off between growth and mortality (Werner and Anholt 1993). Increased activity can lead to increased resource acquisition (and therefore, growth) but may also come at a cost, by increasing susceptibility to predation. At the level of populations, activity is manifest through levels of intraspecific competition between life history stages (*e.g.*, between juveniles, sub-adults, and adults) or through interspecific competition between sympatric species competing for similar resources (Werner 1992). For example, two species which overlap in feeding or habitat niche can avoid direct competition if their populations exhibit non-overlapping activity cycles.

Octopuses are an important mid-level trophic component of many shallow continental shelf marine ecosystems, as both generalist predators on many smaller fish and invertebrate prey (Fawcett 1984, Ambrose 1986) and as important prey items for larger fish and marine mammals (Hanlon and Messenger 1996, Forsythe and Hanlon 1997). Many of these predator/prey relationships should influence, and be influenced by, the activity cycles of their constituent organisms (*e.g.*, Richardson 2001). For example, fish, octopus, and/or other invertebrate predators could be a major selective force shaping (but also responding to) the general activity cycles of fish, octopus, and/or invertebrate prey populations (Daido 2002). Understanding activity cycles of octopuses at multiple life-history stages (*i.e.*, juvenile, sub-adult, and adult stages) may therefore contribute to our understanding of the structuring of resource use among populations and ecological communities in shallow, near-shore marine environments.

Reports of activity cycles in octopuses are scarce, but several species have been studied and characterized as having a basic endogenous day, night, or crepuscular activity pattern. At least some populations of several species of octopus are nocturnal (*Enteroctopus dofleini* (Wülker, 1910): Hartwick *et al.* 1984; *Octopus joubini* Robson, 1929: Mather 1984; *Octopus macropus* Risso, 1826: Meisel *et al.* 2006), whereas other species show a tendency towards diurnal patterns of activity (*Octopus cyanea* Gray, 1849: Forsythe and Hanlon 1997, Hanlon *et al.* 1999). Some species (*e.g.*, *Octopus vulgaris* Cuvier, 1797) may be characterized by populations or individuals which can be nocturnal, diurnal (Wells *et al.* 1983, Meisel *et al.* 2006), and, under certain conditions, arrhythmic (Wells *et al.* 1983, Meisel *et al.* 2003). Overall, these previous studies illustrate substantial variation within and among species and populations of adult octopuses. Unfortunately, there is little information regarding activity cycles of juvenile octopuses of any species, probably due to their small size and highly cryptic nature in the wild.

Octopus bimaculoides Pickford and McConnaughey, 1949 occurs in shallow continental-shelf regions of central California to Baja California, Mexico, where it inhabits rocky reef, kelp forests, and mudflats (Lang 1997). Currently, most observations of *O. bimaculoides* have come from laboratory studies (Forsythe and Hanlon 1988a, Sinn *et al.* 2001); only one study has reported limited *in situ* observations (Lang 1997). Like most shallow-water octopuses, *O. bimaculoides* has a short lifespan (Forsythe and Hanlon 1988b). Adult female *O. bimaculoides* lay numerous (Forsythe and Hanlon 1988a, 1988b), large teardrop-shaped eggs (3-4 mm long) from which relatively well-developed benthic hatchlings are produced after an incubation period of 6-8 weeks. Upon hatching, juveniles disperse by crawling or swimming (as opposed to solely relying on ocean currents). Little is known about the foraging ecology of juveniles in this species, but in laboratory settings juveniles are generalist feeders and will take small shrimp, crabs, bivalves, fish, and gastropods (Forsythe *et al.* 1984, Sinn 2000). There have been no systematic reports of activity cycles in any life stage of *O. bimaculoides*.

The aim of the current study was to determine whether juvenile *Octopus bimaculoides* displayed patterns of activity cycles which could be described as crepuscular, nocturnal, or diurnal under semi-natural laboratory conditions (*i.e.*, natural day lengths and *ad libitum* feeding).

MATERIALS AND METHODS

Brooding female specimens of *Octopus bimaculoides* were obtained commercially from the wild (Chuck Winkler, Long Beach, California) in September 1998 and shipped to Portland, Oregon, where they were maintained until eggs hatched. Two broods hatched synchronously during the week of October 15, 1998, and the majority of individuals hatched within 3-4 days of this date. Within 2-3 days of hatching, octopuses from these two broods were assigned randomly and in equal numbers to two separate holding tubs where they remained until the end of experiments. Holding tubs were 76-L fiberglass tubs (1 m × ⅓ m × ⅓ m) in-line with a 1900-L closed-seawater system. Salinity (34-36 psu) and temperature (18 °C) were held constant throughout experiments. The system had overhead fluorescent lighting in addition to natural, direct sunlight from a large bank of adjacent windows. To allow for diffuse dawn and dusk periods, the day/night light cycle of the fluorescent lights was timed to come on one hour after sunrise and turned off one hour before sunset. Sunrise/sunset times were based on data for Portland, Oregon from *The Astronomical Almanac Online* (U.S. Naval Observatory and H.M. Nautical Almanac Office; http://asa.usno.navy.mil/). Low-powered red lights (25 W), which were never turned off, allowed observations during nighttime hours. Holding tubs contained crushed oyster shell substrate and plastic seagrass beds along with shelter in the form of clay pots, small PVC tubing, and rocks. Hatchling/juvenile octopuses were fed *ad libitum* during non-observation days with littorinid snails (*Littorina scutulata* Gould, 1849), mysid shrimp (*Mysis* spp.), and small shore crabs (*Hemigrapsus* spp.). Juvenile specimens of *O. bimaculoides* have high mortality rates relative to adults (Forsythe *et al.* 1984). Therefore, in order to enhance survival, an attempt was made to maintain at least one type of food source in tubs at all times.

A single 24-hr long observation period on both tubs of octopuses began on October 29, 1998 ($N = 98$ octopuses), when animals were approx. 14 days old. Subsequent 24-hr long observation periods were made on November 11, 1998 ($N = 88$ octopuses) and November 17, 1998 ($N = 87$ octopuses). For each 24 hr period, counts of 'active' octopuses were made on each tub once per hour at the beginning of each hour, beginning at 5 PM on each date. An octopus was considered 'active' if it was crawling, swimming, or sitting outside of cover (at least 50% of its body). The number of 'inactive' octopuses for each count was calculated by subtracting the number of active octopuses counted from the total number of animals within each tank, which had been assessed the day previous to observations by removing all cover and counting total octopuses. The proportion of octopuses active across both tubs was then calculated by dividing the total number of active animals by the total number of active and inactive animals. This method resulted in twenty-four observations per tub per observation day.

A nocturnal versus diurnal activity cycle was tested by examining the proportion of active individuals during daylight hours (7 AM to 5 PM) versus nighttime ones (5 PM to 7 AM) for each week. To examine whether octopuses were crepuscular, mean proportions of active individuals were compared across two time periods for each week, the first representing dawn/dusk periods (6 AM to 8 AM and 4 PM to 6 PM) and the second period representing all other hours (8 AM to 4 PM and 6 PM to 6 AM). Temporal autocorrelation between observations within a tub and an unbalanced statistical design precluded use of hypothesis tests. For example, activity at one observation period was probably not independent of activity during another, and 6 observation times were taken to compute a mean proportion for dawn/dusk activity while 18 observations were used to compute mean activity during 'all other times'. Thus, for statistical comparisons, the mean proportion of active octopuses for the appropriate time period was calculated for each week and graphed along with 95% confidence intervals. Non-overlapping 95% confidence intervals of means were used as a conservative estimate of statistically significant differences because a comparable statistical test would always indicate a statistically significant difference at $P < 0.05$ for two non-overlapping 95% confidence intervals (Payton *et al.* 2003).

RESULTS

There was little evidence to support a crepuscular activity cycle in juvenile *Octopus bimaculoides*. The mean proportion of octopuses active during dawn/dusk periods and all other time periods was not different for any of the three observation weeks (Fig. 1). Instead, juveniles on average exhibited nocturnal activity cycles, as the mean proportion of

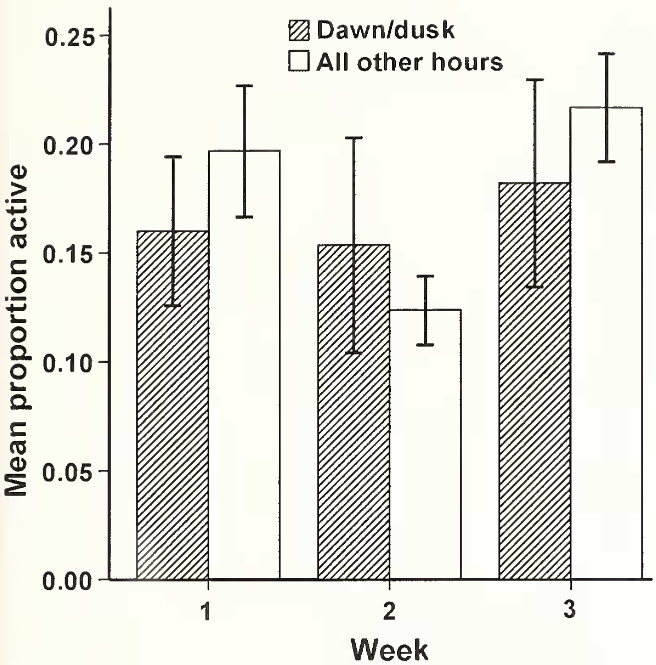

Figure 1. Mean proportion of active juvenile *Octopus bimaculoides* during dawn/dusk (6 AM to 8 AM and 4 PM to 6 PM) versus all other time periods over three weeks. Error bars represent 95% confidence intervals.

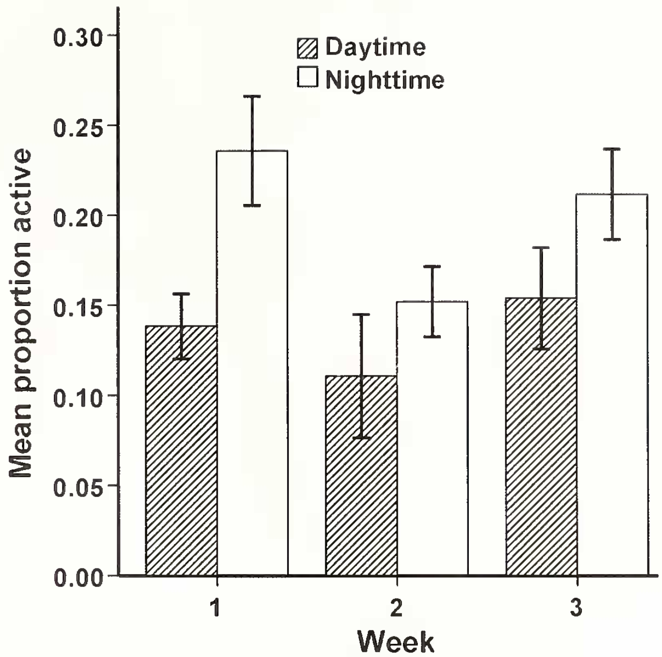

Figure 2. Mean proportion of active juvenile *Octopus bimaculoides* during nighttime hours (5 PM to 7 AM) versus daylight hours (7 AM to 5 PM) over three weeks. Error bars represent 95% confidence intervals.

active juvenile octopuses was greater during nighttime hours than daylight ones in two out of the three weeks (Fig. 2). The activity cycles could be characterized qualitatively each week by an increase in activity which coincided with sunset periods; this activity generally peaked at midnight, after which time there was a steady decrease in activity until the next day's sunset (Fig. 3).

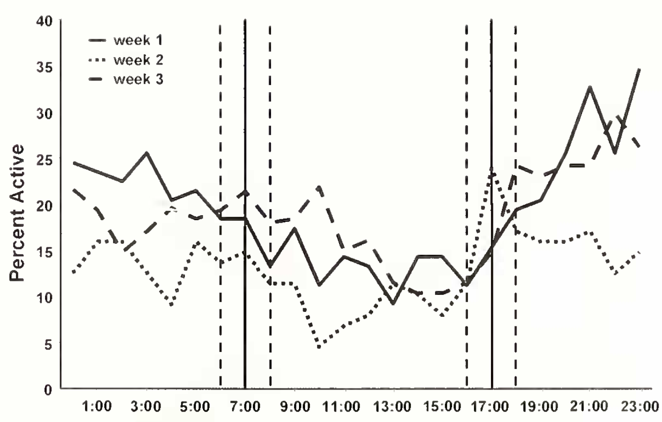

Figure 3. Percentage of juvenile octopuses that was active during each 5-minute monitoring period during each hour. Solid vertical lines represent average sunrise (mean = 7:01 AM, *SD* = 13 min) and sunset (mean = 4:48 PM; *SD* = 12 min). Dashed vertical lines represent dawn (6 to 8 AM) and dusk (4 to 6 PM) periods. Sample sizes varied by week (week 1: $N = 98$; week 2: $N = 88$; week 3: $N = 87$).

DISCUSSION

This is the first report of activity cycles in juvenile California two-spot octopuses, *Octopus bimaculoides*. Under natural daylight conditions and constant food availability, juvenile animals tended to be nocturnal in their activity. This tendency could be potentially adaptive for individuals if predation risk for juvenile octopuses were greater in daylight than nighttime. High numbers of visual predators active during daylight hours (*e.g.*, teleost fish) may favor juvenile octopuses which are active during nighttime hours (Aronson 1991, Hanlon and Messenger 1996). However, intra- and interspecific competition with other octopuses through niche overlap should also influence activity cycles and would favor temporal spacing of time budgets between populations (Houck 1982, Meisel *et al.* 2006). *Octopus bimaculoides* occurs sympatrically along its range with *Octopus bimaculatus*, and these two sister species most likely occupy similar niches (Pickford and McConnaughey 1949). Some populations of adult *O. bimaculatus* can be nocturnal (Ambrose 1982), and nocturnal activity in adult *O. bimaculoides* in the laboratory has also been observed (Sinn 2000). Taken together, these reports suggest that juvenile *O. bimaculoides* may face multiple, conflicting selection pressures influencing their activity patterns. Clearly, further work is needed on the relative influences of predation risk and niche overlap on the activity cycles of juvenile octopuses.

Even in daytime periods, at least some octopuses were active, and during one observation week, there were no differences between activity in daytime and nighttime hours. One explanation could be that metabolic demands for fast-growing juvenile cephalopods are high (Lee 1994), requiring animals to feed throughout a 24-hr cycle. Two other environmental cues which may have influenced the activity cycles of juvenile octopuses, namely food availability and octopus density, are also worth further consideration. For example, food availability influences adult activity in other *Octopus* species, with *ad libitum* feeding resulting in a lack of a discernable 24-hr cycle in adult *Octopus vulgaris* (Wells *et al.* 1983). While constant food availability was chosen here to maximize juvenile survivorship, in the wild, food availability may not be limiting for juvenile octopuses (*e.g.*, *O. bimaculatus*: Ambrose 1988). Second, octopus densities may also have influenced individual activity cycles if densities in tubs were unnaturally high. Increased density may have increased aggressive interactions with conspecifics during peak activity hours (*i.e.*, nighttime) and resulted in some individuals becoming active during daylight (*e.g.*, Sinn *et al.* 2001). Nothing is known concerning natural densities of juvenile *O. bimaculoides*, but adult individuals of *O. bimaculoides* have been reported to spatially group in high densities in suitable habitat in the wild (Lang 1997).

From a practical standpoint, the environmental circumstances experienced by octopuses in the current study were probably similar to culturing conditions other researchers employ when studying juvenile octopuses (*i.e.*, constant food availability to ensure low mortality rates). Understanding the basic activity cycles of laboratory animals is necessary to properly perform experimental manipulations and to recognize 'abnormal' behavior which could indicate sick or dying animals (Moltschaniwskyj *et al.* 2007). Unfortunately, detailed study of cryptic, juvenile octopuses in the wild will probably remain intractable for some time. Therefore, inferences based on laboratory reports, taken with caution, remain the sole information available to understand the interaction between circadian rhythms and the juvenile ecology of many *Octopus* spp.

This study is a first step toward quantifying activity cycles in the juvenile life stages of *Octopus bimaculoides* and provides a baseline for studying juvenile life stages both in the laboratory and field. Understanding the activity cycles of different life-history stages of *Octopus* spp. under natural or semi-natural conditions should contribute to our understanding of the ecological costs and benefits that arise from an animal taking a particular activity strategy under a given set of conditions (Sinn *et al.* 2001). Further work is clearly needed on the influences of competition and predation risk on octopus activity cycles and the resulting population- and species-specific outcomes (Ambrose 1982, 1986).

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